"Proboscis pores" in Craniate Vertebrates, a Suggestion concerning the Premandibular Somites and Hypophysis.

By

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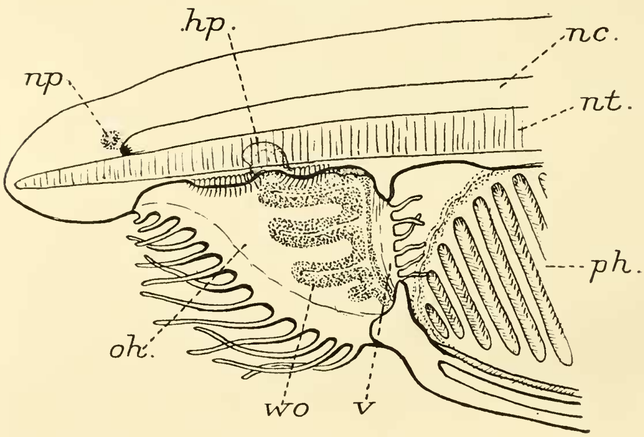
With Plate 28, and 3 Text-figures.

THERE is in Amphioxus on the roof of the buccal cavity a deep pit known as Hatschek's pit, from its discoverer. Its blind, inner end extends upwards to the right of the notochord, while the lining epithelium is continuous at the opening of the pit with the areas of thickened ciliated epithelium which spread over the roof and sides of the buccal cavity. This ciliated organ is the wheel-organ of Johannes Müller, and was shown by him to drive a current of water and food-particles into the mouth. Van Wijhe (**14**) has since given a detailed account of its structure. An unpaired dorsal region extends backwards so as to surround the opening of the pit, then divides into right and left tracts. The two branches run towards the velum and then down the sides of the buccal cavity, but do not meet ventrally. As shown in Text-fig. 1, finger-shaped tracts extend forwards on the inner surface of the oral hood. These structures become more complicated in older specimens. The deeply staining epithelium of which Müller's organ is composed is formed of very closely packed, narrow columnar cells, whose nuclei form several layers, and whose outer ends bear each one cilium. Good figures of these cells have been given by Langerhans (**8**).

Although the pit and its lining epithelium have been described by several authors—Hatschek (**6**), Langerhans (**8**), Willey (**16**), van Wijhe (**14**), Andrews (**1**)—the complexity of its histological elements seems to have escaped the notice of these observers, and its finer structure deserves further study. In the adult the epithelium is composed of cells roughly disposed in three layers (Pl. 28, figs. 12, 13, 14). The most superficial cells are large, with a broad end reaching to the

Text-fig. 1.



Left side-view of the head of a young Amphioxus. The left body-wall, oral hood, and wall of the pharynx have been cut away, exposing the right half of the wheel-organ, *w.o.* Hatschek's pit, *H.p.*, is seen by transparency. *n.c.* nerve cord. *n.p.* Olfactory pit. *n.t.* Notochord. *o.h.* right oral hood. *ph.* Pharynx. *v.* Velum surrounding the true mouth.

free surface, and bearing a bunch of fine cilia generally gathered together to form a flame-like tuft. Their nuclei are pale and rounded. The middle layer is composed of narrower cells, with oval, deeply staining nuclei. Each of these cells is prolonged to the surface and beyond it into a long, narrow, stiff, rod-like extremity bearing a single stout cilium. The third and simplest variety of cell forms the deepest layer next to the basal membrane covering the organ. The peculiar rod-bearing cells are arranged in four or five transverse rows alternating with the large ciliated cells, and also round the opening of the pit. Here the rods become shorter and shorter, until this type of cell passes into the more ordinary ciliated epithelium of the organ of Müller (Pl. 28, fig. 12).

Hatschek, who noticed the rod-bearing cells, considered the pit to be a sense-organ. But since no nerve can be traced to it, this interpretation is probably incorrect. Andrews states that in Asymmetron the pit secretes a mucous substance, which entangles food-particles and gets carried into the mouth. He points out its relation to the blood-vascular "glomus," and concludes that Hatschek's pit is a slime-secreting gland—a conclusion later supported by van Wijhe.

The story of the origin of Hatschek's pit is one of the strangest episodes in the strange history of the development of Amphioxus. It is a mesoblastic structure formed from the first mesoblastic somite of the left side. Hatschek (**5**) studied the development of the anterior pair of pouches, and correctly described that on the right side as enlarging forwards and downwards so as to give rise to the main head-cavity of the larva. The left pouch he believed became constricted into two portions. One, taking up a position on the right and below the notochord, gave rise to Hatschek's pit itself, while the other opened to the exterior on the left side and gave rise to the preoral pit of the larva (**6**). The larval preoral pit subsequently becomes drawn into the buccal cavity at metamorphosis, and acquires its definitive position in the adult by a process of shifting and overgrowth admirably depicted by Willey (**15**). Hatschek's description of the early development of the pit is by no means clear, and unfortunately is published without figures (**6**). Some years later, Legros (**9**) stated that the sac on the left side of the early embryo was derived, not from a cœlomic pouch, but from an invagination of the ectoderm, and that from it were developed the pit, the ciliated organ, and the anterior nephridium (Hatschek's nephridium).[1] This interpretation of the origin of the sac

[1] This nephridium is developed neither from a mesoblastic funnel, as described by Hatschek (**6**), nor as an outgrowth from the second

was disproved by MacBride (**11**), whose results were accepted by van Wijhe (**14**), and since Legros has recognised his mistake the controversy may be dropped. As, however, it seemed desirable to reinvestigate the whole question, an account is here given of the development of the pit and Müller's ciliated organ from their first appearance to the adult condition.

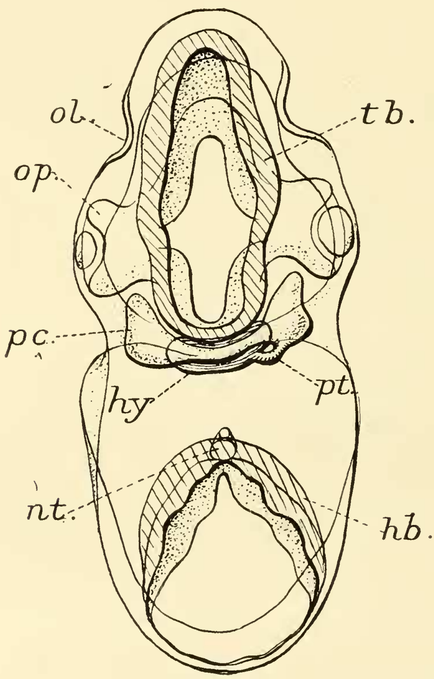
The first pair of cœlomic sacs are given off as lateral pouches at the extreme anterior end of the archenteron, and can be seen in embryos about twenty-four hours old still in this condition (Pl. 28, fig. 3). Later the pouches become nipped off, and come to lie symmetrically on either side of the notochord (Pl. 28, fig. 2). Even in these very early stages the left may have a rather thicker wall than the right sac (Pl. 28, fig. 1). At about the 30-hour stage the right sac begins to expand, it walls thin out, and later on it expands to form the head-cavity of the larva. The left sac with its thicker wall at first remains spherical, but later becomes flattened, and takes up a position lying transversely between the notochord above and a backward prolongation of the right head-cavity below (Pl. 28, fig. 5). Its outer end now becomes applied to the ectoderm on the left side. Larvæ about fifty hours old show that an opening has been pierced at this point of contact, placing the cœlom in communication with the exterior. At the same time the large cubical cells lining the cavity acquire cilia (Pl. 28, fig. 6). In larvæ with two gill-slits the left cœlomic sac has enlarged, spreading further towards the right side, while the ectoderm round the opening has grown inwards, tending to form a depression

somite, as described by Legros (**10**); nor, again, from the remains of the communication of the cœlomic pouch with the gut, as alleged by MacBride (**11**), but from a little group of cells appearing quite early just above the mouth. Several years ago I traced these cells to a stage about thirty hours old, before the opening of the mouth; but since I was unable to find out their first origin, I refrained from publishing my results. They are the cells figured recently by Smith and Newth (Pl. 18, fig. 4), who are indeed correct in their surmise that they may represent the rudiment of the nephridium (**13**).

(Pl. 28, fig. 7). Eventually this depression becomes large and deep, forming the preoral pit of the larva (Pl. 28, figs. 8, 9, 10). The lining epithelium becomes modified into the thick ciliated epithelium so conspicuous in later stages, and in the adult wheel-organ developed from it. For it is this preoral pit which is converted into the organ of Müller when the buccal cavity is formed at metamorphosis. Whether the thickened ciliated epithelium lining the preoral pit is actually derived from the ectoderm and not from the Hatschek's pit it is difficult to prove for certain, since the distinction between the mesoblastic cells and the ectoblastic cells at the mouth of the pit soon becomes indefinite. Moreover, there is an unfortunate slight gap in my series between the oldest stage reared in the laboratory at Naples (51 hours) and the youngest free-swimming larva with two gill-slits I was able to obtain at Faro, and it is just at this stage that the proliferation of cells at this point begins. Nevertheless, the appearance in sections of these young larvæ has convinced me that the lining of the preoral pit is indeed of purely ectodermal origin. How, then, can we account for the presence of the rod-bearing cells in the lining of Hatschek's pit itself? As mentioned above, they appear to be a specialised form of the slender cells composing the epithelium of the preoral pit (future wheel-organ). There can be hardly any doubt that the rod-bearing cells invade Hatschek's pit from the outside, and are derived from the epithelium which grows in at the open mouth of the sac. In young larvæ they do not yet occur among the larger mesoblastic cells; but in later stages they can be seen in increasing numbers, first near the opening, and then spreading over the inner surface of the sac.

To sum up concerning the history of the ciliated wheel-organ of Müller and of Hatschek's pit in Amphioxus: The first pair of cœlomic sacs or somites develop as outgrowths, which soon become nipped off from the anterior end of the archenteron. They are at first symmetrical, but soon the right enlarges to form the head-cavity, while the left, remaining comparatively small and thick-walled, acquires an opening to the exterior on the left side, in front of the mouth. The ectoderm round the opening sinks in to form a deep groove and depression—the preoral pit. The cells lining the original left cœlomic sac, now known as Hatschek's pit, are broad, with a rounded nucleus and a bunch of cilia. The

Text-fig. 2.



Reconstruction from transverse sections of a thick slice of the head of an embryo of Torpedo, 10·5 mm. long. Anterior view. *f.b.* Forebrain. *h.b.* Hindbrain. *h.y.* Hypophysis. *n.t.* Notochord. *o.l.* Olfactory sac. *o.p.* Optic cup. *p.c.* Premandibular somite. *p.t.* Premandibular tube, or canal opening into the hypophysis.

cells lining the preoral pit are probably of entirely ectodermal origin, and acquire a slender, elongated shape with an oval, deeply staining nucleus and a single flagellum. In later stages they appear to invade the pit of Hatschek, becoming specialised into the rod-bearing cells. As the larval mouth becomes transformed into the adult mouth, and the lateral flaps of the oral hood develop, the preoral pit is carried into the buccal cavity, where it flattens out and spreads to form the ciliated organ.

Now in Balanoglossus the first pair of cœlomic sacs arise in essentially the same way, and acquire an opening to the exterior known as the proboscis pore. As in Amphioxus, so in B. kowalevskii, the pore is formed only on the left side. In B. kupfferi, however, both a right and a left pore are present. More than thirty years ago Bateson, in his important papers on the development of Balanoglossus, compared the opening of Hatschek's pit in Amphioxus with the proboscis pore (2), and further suggested that the proboscis pore and gland of Balanoglossus correspond to the hypophysis and pituitary gland of the Craniata. A discussion of the latter interesting suggestion would require a detailed study of the structure and development of these parts in Balanoglossus —a subject into which we need not enter here; but Bateson's comparison of the pores seems to be strongly supported by the facts mentioned above. The homology may, of course, be extended to the similar pores in Cephalodiscus, and to the water pores of Echinoderms.[1]

Turning now to a comparison between Amphioxus and the Craniate Vertebrates. That the hypophysis is an ancient organ which must have been possessed by the ancestor of all Craniates is shown by its constant presence and uniform development. Invariably it arises as an ingrowth of ectoderm just in front of the mouth and just anterior to the front end of the archenteron.[2] From the wall of the latter are here

[1] A comparison with the Tunicata is much more difficult. We can hardly avoid the conclusion that the subneural gland with its ciliated duct and dorsal tubercle are homologous with the hypophysis; but of anterior cœlomic sacs and of proboscis pores in Ascidians we know nothing as yet. On the other hand, it is possible that further research may reveal traces of these organs in some of the less modified forms.

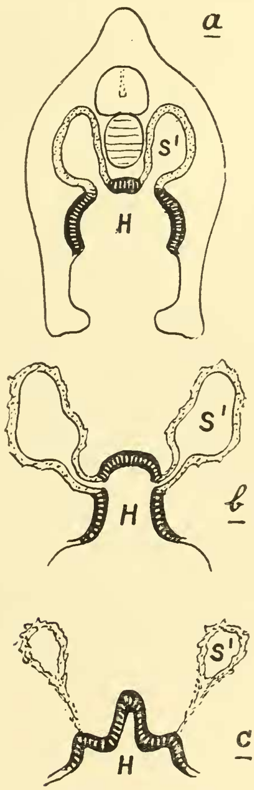
[2] For an excellent account of the development of the hypophysis and a review of the literature see the recent papers of E. A. Baumgartner in the 'Journal of Morphology,' vols. 26, 1915, and 28, 1916.

produced the anterior extremity of the notochord, and the lateral outgrowths which give rise to the first pair of somites or anterior premandibular cavities of Balfour. In spite of the doubts raised by Hatschek (**6**) and von Kupffer (**7**), it is now generally admitted that the proboscis cavities of Balanoglossus, the anterior sacs of Amphioxus, and the premandibular cavities of Craniates are all homologous structures representing the first pair of cœlomic somites (Willey (**15**), MacBride (**11**)).

No satisfactory explanation of the origin of the hypophysis has yet been arrived at. Beard, Dohrn, and others have suggested that it represents a vestige of the original mouth, a new mouth having been developed from gill-slits. But the fundamental correspondence in the structure and relations of the mouth and associated parts in the Ascidian, Amphioxus, and the Ammocœte larva, and many other facts which need not be mentioned here, render this view in the highest degree improbable. Many authors have sought in Amphioxus for the homologue of the hypophysis; but, strangely enough, most of them profess to find it in the neuropore or olfactory pit of Kœlliker. For this theory, suggested by Hatschek (**6**), and strongly supported by Willey (**15**), there seems to be no justification. Since both neuropore and hypophysis coexist in the embryo Craniate, are situated widely apart, and are related to quite different regions of the brain, it is difficult to see how they could correspond to the olfactory pit. On the other hand, the much more plausible comparison of the hypophysis with the wheel-organ of Amphioxus has received little attention. It is true that Legros at one time maintained that Hatschek's nephridium, Hatschek's pit, and the wheel-organ correspond to the hypophysis and olfactory pit of Craniates (**9**); but this view was based, as already mentioned above, on erroneous observations, and has since been abandoned.

There is strong evidence to support the theory of the homology of the hypophysis with the wheel-organ of Amphioxus (the preoral pit of the larva). Were it not for the excessive prolongation forwards of the notochord in Amphioxus, they would both appear as ectodermal organs situated below the brain and in front of the mouth. If we restored the bilateral symmetry of the head in Amphioxus, both the

TEXT-FIG. 3.



Diagrams of transverse sections through the premandibular region of the head of *a*. Amphioxus (restored to a bilaterally symmetrical condition). *b*. Torpedo. and *c*. The Reptile Gongylus (from the figures of Salvi). *H*. Hypophysis. S^1. Premandibular somite, or first anterior cœlomic sac.

right and the left anterior cœlomic sacs would open into this ciliated depression as shown in Text-fig. 3A, and there would be two "proboscis pores." Now the suggestion I wish to make in this paper is that there is direct evidence of the existence of two such "proboscis pores" opening into the hypophysis of the Craniate Vertebrates. If the evidence be accepted it will, naturally, greatly strengthen the theory that the hypophysis and the wheel-organ are homologous structures.

Chiarugi, in 1898 (**3**), was, I believe, the first to mention a connection between the premandibular somites and the hypophysis in Torpedo. Since then Dohrn has carefully described this connection in embryos of Torpedo ocellata and marmorata, and of Raja batis (**4**). It is a transient structure, but when best developed consists of a tubular extension of the premandibular somite passing downwards to the posterior wall of the hypophysis, and placing the premandibular cavity in communication with the lumen of the hypophysis (Text-fig. 3B). Just as in Balanoglossus, an Echinoderm, or Amphioxus, the anterior cœlomic sac grows towards and fuses with the ectoderm to form the "proboscis" or "water" pore, so in the Elasmobranch this tube grows out of the premandibular somite and fuses with the hypophysial ingrowth. There may be a right and a left tube, but—a significant fact—the left is usually better developed and persists longer than the right. In Text-fig. 2 a reconstruction is given from a series of sections of Torpedo kindly lent to me by Prof. J. P. Hill, in which Miss Fraser found the tube. In this case it appears to be developed on the right side only. Pl. 28, fig. 15, shows, on a larger scale, the opening into the cavity of the hypophysis.

Similar structures have been described in the Reptilia. Already in 1888 Ostroumoff (**12**) mentioned a paired connection between the premandibular somites and the hypophysis in Phrynocephalus, and the same structure has been independently described in detail in the embryo of Gongylus ocellatus by Salvi (**12a**).

Want of material has prevented my confirming the observations of these authors, but, in the 3-day embryo of the duck, I find the premandibular somites intimately connected with the hypophysis. Probably, if a careful search be made, the premandibular tubes will be found to occur both in birds and in mammals.

Finally, it may be urged that all these openings, water-pores, proboscis pores, and premandibular pores are of the nature of cœlomostomes comparable to the excretory tubules in the more posterior segments of the Craniates. It may also be pointed out that the theory here advocated gives a clue to the first origin and function of the hypophysis.[1]

Summary.

An account is given of the complex histological structure of the epithelium lining Hatschek's pit in Amphioxus, and of the development of this pit and of the preoral pit from the left anterior cœlomic sac and an ectodermal ingrowth respectively. The preoral pit becomes the wheel-organ of the adult. The ciliated cells of Hatschek's pit are of mesodermal origin, but the rod-bearing cells appear to come from the ectoderm. The evidence is strongly in favour of Bateson's comparison of the opening of Hatschek's pit with the proboscis pore of Balanoglossus and the water-pore of Echinoderms. All these pores were originally paired. The anterior cœlomic sacs of Amphioxus are homologous with the premandibular somites of Craniates. As shown by Ostroumoff, Dohrn, and Salvi, these somites form tubular outgrowths opening into, or fusing with, the hypophysis—a connection comparable with the "proboscis" pores of Enteropneusta, Cephalodiscus, and Echinodermata. The premandibular, proboscis, and water-pores are all of the nature of cœlomostomes. It is concluded that the hypophysis of the Craniata is represented in Amphioxus by the wheel-organ situated in front of the true mouth, and that its original function was probably to drive food into the alimentary canal.

[1] An abstract of this paper was read at the meeting of the Linnean Society held on April 19th, 1917.

Postscript.

Since this paper was printed I have again come across some interesting work which had unfortunately escaped my memory, but to which attention must be drawn, as it has an important bearing on the questions dealt with above. I refer to the papers on "Amia" by Phelps ('Science,' vol. ix, 1899), by Reighard and Phelps ('Journ. of Morph.,' vol. xix, 1908), and by Eycleshymer and Wilson ('Biol. Bull.,' vol. xiv, 1908), and on "Polypterus" by Kerr ('Budgett Mem.,' 1907). These authors trace the development of the adhesive or cement organ of the larva from paired diverticula of the anterior end of the archenteron. Each diverticulum becomes nipped off, and subsequently acquires an opening to the exterior. The adhesive organs of Lepidosteus and Acipenser are probably of the same nature. Now, while Kerr is unwilling to commit himself to any theory of the homology of these organs, but nevertheless indicates "the probability that they correspond with the premandibular head-cavities," Reighard and Phelps definitely compare the pouches which give rise to the adhesive organs to the so-called anterior head-cavities found by Miss Platt in Acanthias, and supposed to represent a pair of somites in front of the premandibular somites of Balfour. Following Neal ('Bull. Mus. Comp. Zool.,' vol. xxxi, 1898) they further homologise these anterior head-cavities with the first pair of somites in Amphioxus (the left one of which opens to the exterior), and suggest that they and the adhesive organs may be homologous. This comparison, however, raises a serious difficulty. If the anterior head-cavity really represents a separate segment, then the segmental correspondence between the first pair of somites in Amphioxus and the premandibular somites in higher vertebrates would seem not to hold good. Since no somite has been found in Petromyzon in front of the premandibular, we may be forced to the conclusion that the whole cephalic structure has been transposed one segment back in the Gnathostomata (see "Segmentation and Homology," this journal, vol. lix, 1913). Such a conclusion is by no means inadmissible, but does not appear to be necessary. As a matter of fact no definite trace of an anterior head-cavity has been seen in any other group but the Selachii (adhesive organs apart), and it is not constant even in them. On this point the very careful work of Dohrn (**24**) seems to me convincing. Many authors do not admit its homology with a somite (v. Wijhe, Dohrn); rather would the walls of the cavity seem to be derived from the premandibular segment, and to represent merely a specialised region of its somite.

If, then, the anterior head-cavity really belongs to the premandibular segment, and if it is represented in these Teleostome larvæ by the adhesive organ, the remarkable conclusion is reached that not only in Cephalochordates, Selachians, and Reptiles is there evidence that the first pair of somites opened on the lower surface of the head (either on or near the hypophysial depression), but that this is still the case in some Teleostomes.

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EXPLANATION OF PLATE 28,

Illustrating Mr. Edwin S. Goodrich's paper on "Proboscis Pores in Craniate Vertebrates, a Suggestion concerning the Premandibular Somites and Hypophysis."

Reference Letters of Plate Figures.

a. Elongated rod-cell. *ace.* Anterior ciliated epithelium of wheel-organ. *acg.* Anterior ciliated groove. *b.* Ciliated cell. *blv.* Blood-vessel. *ca.* Premandibular tube or canal. *cb.* Basal canal. *cHn.* Cœlom of second somite, into which projects Hatschek's nephridium. *de.* Ectoderm dorsal to preoral pit. *ebc.* Epithelium of buccal cavity. *end.* Endostyle. *ent* Enteron. *Hn.* Hatschek's nephridium. *Hp.* Hatschek's pit. *hyp.* Hypophysis. *inf.* Infundibulum. *la.* Left aorta. *lbf.* Left buccal fold or oral hood. *lc.*[1] and *lc.*[2] First and second left cœlomic cavities. *ls.*[1] and *ls.*[2] First and second cœlomic sacs or somites. *m.*[1] and *m.*[2] First and second myotomes. *nc.* Nerve cord. *np.* Neuropore. *npl.* Neural plate. *nt.* Notochord. *pce.* Posterior ciliated epithelium of wheel-organ. *pcg.* Posterior ciliated groove. *pm.* Preoral muscle. *pmd.* Premandibular somite. *pos.* Preoral sense-organ. *rbc.* Roof of buccal cavity. *rbf.* Right oral hood. *rc.*[1] and *rc.*[2] Right first and second cœlomic cavities. *rs.*[1] and *rs.*[2] Right first and second cœlomic sacs or somites. *ve.* Ectoderm ventral to preoral pit.

PLATE 28.

Figs. 1–14 are of Amphioxus.

Fig. 1.—Transverse section through anterior region and neuropore of a 24 hours' old embryo. Cam. W., 2 mm., oc. 3.

Fig. 2.—Similar section through a more advanced embryo, 24 hours old. Cam. W., 2 mm., oc. 3.

Figs. 3 and 4.—Transverse sections through an embryo 24 hours old. Fig. 3 shows the anterior somites, fig. 4 only the second pair of somites. Cam. W., 2 mm., oc. 3.

Fig. 5.—Transverse section through an embryo 30 hours old. Cam. W., 2 mm., oc. 3.

Fig. 6.— Transverse section through a larva 48 hours old, with Hatschek's pit opening to the exterior. Cam. W., 2 mm., oc. 3.

Fig. 7.—Portion of a transverse section of a larva with two open gill-slits, showing Hatschek's pit and the preoral sense-organ. Cam. W., 2 mm., oc. 3.

Fig. 8.—Transverse section of an older larva. Cam. W., 2 mm., oc. 3.

Fig. 9.—Portion of a transverse section of an older larva, showing the developing preoral pit and groove.

Fig. 10.—Section of the same larva farther forward. Cam. W., 2 mm., oc. 3.

Fig. 11.—Portion of a transverse section of the buccal region of an old larva in which the atrium has developed. Cam. W., 2 mm., oc. 2.

Fig. 12.—Longitudinal vertical section through Hatschek's pit in an adult. Cam. Z.D., oc. 2.

Fig. 13.—Transverse section through Hatschek's pit in an adult. Cam. Z.D., oc. 2.

Fig. 14.—Enlarged view of a portion of a section of the epithelium lining Hatschek's pit in the adult.

Fig. 15.—Portion of a transverse section of the head of an embryo of Torpedo 10·5 mm. long. The entrance of the premandibular tube or canal, *ca*, into the hypophysis is shown.